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Morphological Differences Among Juvenile Coho Salmon *Oncorhynchus Kisutch* Living in Nearby Tributaries of a Small Coastal Watershed

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ABSTRACT

Bailey, R. E. and J. R. Irvine. 1991. Morphological differences among juvenile coho salmon Oncorhynchus kisutch living in nearby tributaries of a small coastal watershed. Can. Tech. Rep. Fish. Aquat. Sci. 1780: 15 p.

We used truss network analyses to test for differences in body morphology among groups of juvenile coho salmon from five riverine environments within the Keogh River watershed on northern Vancouver Island. Shape differences were found which may have been due to phenotypic plasticity, genetic polymorphisms, ontogenetic differences, genetic isolation, or chance. Fish from one tributary (Misty Outlet stream) had larger dorsal, anal, and caudal fins and a smaller caudal peduncle region than fish of similar lengths from three other tributaries, and fish from the mainstem Keogh River had smaller fins and a larger caudal peduncle region than fish from the other sites. We were unable to demonstrate a relationship between the shapes of fish from any particular tributary, and the physical habitat characteristics of that location. Further research is required to determine the reason for the observed differences. If the observed differences are the result of genetic isolation, those entrusted with the responsibility of managing and/or enhancing small populations such as these should attempt to treat such populations as separate stocks if they wish to maintain the existing genetic diversity.

RÉSUMÉ

Bailey, R. E. and J. R. Irvine. 1991. Morphological differences among juvenile coho salmon Oncorhynchus kisutch living in nearby tributaries of a small coastal watershed. Can. Tech. Rep. Fish. Aquat. Sci. 1780: 15 p.

Nous avons utilisé des grilles en treillis pour analyser les différences dans la morphologie corporelle des saumons cohos juvéniles de cinq milieux riverains du bassin versant de la rivière Keogh, dans le nord de l'île de Vancouver. On a constaté des différences morphologiques qui pourraient être dues à la plasticité phénotypique, au polymorphisme génétique, aux différences ontogénétiques, à l'isolement génétique ou au hasard. Les poissons d'un tributaire (Misty Outlet) avaient de plus grandes nageoires dorsale, anale et caudale et un plus petit pédoncule caudal que les poissons de taille similaire de trois autres tributaires, tandis que les poissons de l'axe principal de la rivière Keogh avaient les nageoires plus petites et le pédoncule caudal plus grand que les poissons des autres sites. Nous avons été incapables d'établir une relation entre la forme des poissons d'un tributaire particulier et les caractéristiques de l'habitat. Il faudra poursuivre les recherches afin de déterminer la cause des différences observées. Si ces dernières résultent de l'isolement génétique, les personnes chargées de gérer ou de mettre en valeur les petites populations comme celles-ci devraient tenter de les traiter comme des stocks distincts, s'ils veulent maintenir la diversité génétique existante.

INTRODUCTION

Animals adapt to their environments. Adaptations may be morphological, physiological, behavioral, or some combination therein, and presumably confer an advantage for individuals possessing these traits. Ricker (1970) postulated that adaptations may be environmentally determined, genetically determined, or result from a combination of environmental and genetic factors. Morphological differences among stocks of Pacific salmon have been documented for coho, Oncorhynchus kisutch (Fleming and Gross 1989), chinook O. tshawytscha (Beacham et al. 1989), chum O. keta, and pink O. gorbuscha (Beacham and Murray 1985). The morphological differences found in chum salmon may be used with meristic and electrophoretic traits for stock specific management (Fournier et al. 1984).

Morphological differences have been related to habitat and stock type (hatchery or wild). Bisson et al. (1988) found morphological differences among three species of stream-resident salmonids, and related these differences to the habitat utilized by each. Hjort and Schreck (1982) reported that juvenile coho salmon from similar environments were more alike in body shape than those from differing habitats. Hjort and Schreck (1982) also noted discrepancies between the shapes of hatchery and wild coho salmon. Morphological differences have been found among hatchery stocks of chinook salmon (Winans 1984), and among populations of juvenile Atlantic salmon, Salmo salar (Riddell and Leggett 1981) and coho salmon (Taylor and McPhail 1985) rearing in headwater and coastal tributaries of large watersheds.

Since juvenile coho salmon typically spend one year in freshwater before migrating seaward (Hart 1973), they have developed adaptations to their early freshwater environment. Swain and Holtby (1989) described behavioral and shape differences between juvenile coho living in a lake and those living in a tributary to the lake. To date however, it has not been determined whether morphological differences exist among coho parr from separate tributaries within a small watershed, and whether differences are due to genetic or environmental factors. It is necessary to determine the role of environment and heridity if we wish to maximize genetic diversity in stocks that we manage and enhance.

The primary objective of this study was to test for differences in body shape among coho salmon parr from five nearby riverine sites within a single drainage basin, using truss network analysis. Where morphological differences were found among groups of fish from different sites, we then wished to explore possible relationships among the morphological traits present in the fish at the various sites, and the physical habitat characteristics of those sites.

MATERIALS AND METHODS

FISH POPULATION SAMPLING AND DATA COLLECTION

Juvenile coho salmon were collected from five lotic environments within the lower Keogh River watershed on northern Vancouver Island, British Columbia. General descriptions of the study watershed are provide in Swales et al. (1988), Ward and Slaney (1988), and Irvine and Ward (1989). Of the five locations, two; (Misty Outlet Creek (MO), and Long Outlet Creek (LO)), are outlets of lakes, and flow into the Keogh River about 10 km and 12 km upstream from the ocean, respectively. West Tributary (WT), a tributary of the Keogh River, flows into the Keogh River about 4 km above the tide; the tributary stream of West Tributary (WTT) flows out of a series of ponds and beaver dams, then descends for about 200 m prior to joining WT about 1 km upstream from its confluence with the Keogh River. The other sample location was the Keogh River mainstem (KEO), immediately upstream of the Highway 17 bridge crossing, approximately 1.5 km above the entry of LO, and about 14 km upstream from the ocean (Fig. 1).

To permit an examination of possible relationships among fish morphology and habitat, physical attributes of the five sample locations were documented. Water depth, mid-column water velocity, and substrate particle type (Bovee and Cochnauer 1977) were recorded for the locations where fish were captured. The range of widths was determined for the entire stream in the vicinity of fish capture. Water staining was determined by measuring light absorbance compared to a distilled water standard (at 400 nm) of a filtered (0.45 u) water sample from each site. Gradient was estimated for each of the systems from a 1:50,000 topographic map (Dept. of Energy, Mines, and Resources, Ottawa; Sheet 92L/11). Gradients for LO and MO could not be estimated accurately because contour lines on the topographic map did not intersect these tributaries at appropriate locations. No statistical comparisons were made among sites for any physical habitat parameters.

Fish were collected August 8 to 11, 1988, using "Gee" minnow traps (Cuba Specialty Manufacturing Co.) (Swales 1987). Traps were baited with approximately 20 g of salted salmon roe which was wrapped in multiple pinholed plastic bags. The bait was placed in bags to prevent ingestion by the fish, which may have resulted in temporary changes to body shape. Traps were left for 18-24 hr, then fish were removed. Recently emerged fry were also sampled during spring, 1989. However, spring catches at some sites were very low, and the size range of the fish captured was very large, so these results are not included in this paper.

Upon removal from the traps, fish were anaesthetized using 2-phenoxyethanol and photographed using an single lens reflex camera equipped with a 50 mm lens and an accessary close-up lens. The camera was mounted on a stand to ensure that the angle of view, and the distance from the fish,

remained constant. After recovering from the anaesthetic, all fish were liberated at the site from which they were captured. Films (Kodak TMax, 400 ASA) were developed, and actual size prints were made of each fish.

We used truss network analysis (Winans 1984) to determine whether differences in body shape existed among the groups of fish captured at different sites. With this method, the network of trusses (inter-landmark distances) along the fish forms a regular series of contiguous quadrilaterals or cells that describe body shape (Strauss and Bookstein 1982).

Truss measurements were made using the fish pictures, heavy paper, and a digitizing pad. Each fish print was placed on a piece of thick paper and the locations of 17 landmarks (+/- 0.25 mm) were marked on the paper by inserting a pin through the photograph into the paper. The 17 landmarks included the 14 external points of Winans (1984), plus the fork of the caudal fin, and the distal tip of the longest ray of each of the dorsal and anal fins (Fig. 2). We included the additional measurements of fin size because observations of coho fry in the field (Irvine and Bailey; unpublished data), and the recent work of Swain and Holtby (1989), indicated that fin sizes were potentially important discriminators of groups of coho. All points were digitized using a digitizing pad (GTCO Corporation) and the data entered into a micro-computer for analysis. Thirty-one inter-landmark (truss) measurements, the lengths of the lead rays of the dorsal and anal fins, and forklength were calculated using the X-Y positions of the landmarks, and the Pythagorean theorem.

STATISTICAL ANALYSES

Forklength (FKLEN) (inter-landmark distance 2-14) (Fig. 2) frequency histograms (SAS Institute 1988a) were constructed for the fish from each location. For all locations, bimodal distributions were found. Scale ageing of other summer samples of juvenile coho from various Keogh River tributaries determined that the upper modes were composed of mostly 1+ fish (J. R. Irvine; unpublished data). To reduce the chance of incorporating fish of other than 0+ age class into our analyses, fish in the upper modes were excluded from further analyses.

Thirty one truss lengths, and the lengths of the lead rays of the dorsal and anal fins were used in morphometric analyses. To describe body shapes, principal component analyses (Humphries et al. 1982; SAS Institute 1988b) were performed. The principal components were calculated from a correlation matrix of the untransformed truss data. The first principal component (PC1) is generally a measure of size, and the second principal component (PC2), if free of size dependence, describes shape (Swain and Holtby 1989). Correlations between PC1 scores and PC2 scores and fork length were computed to test for size dependency. Correlations between PC2 scores and individual truss length and fin measurements were then determined to identify those characters that were significantly influencing PC2 scores.

To ascertain if significant differences in shape existed among fish from the five sites, mean PC2 scores for each site were compared using analyses of variance (ANOVA). When significant differences were found, the means were tested for intergroup differences using Tukey's tests (SAS Institute 1988b).

RESULTS

Two hundred and twelve juvenile coho salmon from the five sites in the Keogh River drainage were captured, photographed, and released. Based on the length frequency analyses performed, 50 fish were considered likely to be 1+, and were excluded from further analysis. Photographs of 37 fish from each of MO and LO, 31 from KEO, 29 from WT, and 28 from WTT were retained for analysis of shape differences. Truss and lead fin ray lengths were approximately normally distributed.

PC1 and PC2 accounted for 81.9 and 4.1 percent respectively of the total variability in the morphometric variables. PC1 scores were all positive, varying from 0.104 to 0.189 (Table 2), and the correlations between PC1 and FKLEN were all significant ($P<.05$). PC2 scores ranged from -0.490 for character 9-11 (insertion of anal fin to anterior attachment of the ventral membrane of caudal fin) to 0.451 for 7-16 (the length of the lead ray of the anal fin). PC2 scores were not significantly correlated with FKLEN ($P>.05$) within any group, hence PC2 scores for each group were considered to be independent of size.

Twelve truss characters were significantly correlated ($P<.05$) with PC2 scores (Table 2). With the exception of 9-10, all trusses in cell 5 were correlated with PC2 scores, as were 11-12 (depth of the caudal peduncle), 11-13, (length of the lower edge of the caudal fin), and 12-14 (upper lobe of caudal fin) in cell 6. Only three characters from the four anterior cells were significantly correlated with PC2 scores: 2-4 (snout to beginning of the scaled nape) in cell 1; 6-8 (origin to insertion of the dorsal fin) in cell 3; and 7-9 (origin to insertion of the anal fin) in cell 4. The lengths of the lead rays of the dorsal (6-17) and anal (7-16) fins were the other two significantly correlated characters.

Mean PC2 scores differed significantly among locations (ANOVA; $P<.05$). Fish from MO had the highest mean PC2 score; fish from KEO had the lowest, and fish from both these locations differed significantly from each other, and from fish from WT, WTT, and LO ($P<0.05$; Table 3). Means for fish from WT, WTT, and LO were not significantly ($P>.05$) different from each other. The larger mean PC2 score for fish from MO indicates loading of those characters with large positive PC2 scores, and reduced loading of those with

large negative scores, i. e., larger dorsal, anal, and caudal fins, and a concurrent reduction in the size of the caudal peduncle (cell 5 and 11-12 of cell 6). The lower mean PC2 score for fish from KEO indicates smaller dorsal, anal, and caudal fins, and an increase in the size of the caudal peduncle.

The greatest dichotomy among the study sites occurred between the tributaries and the mainstem Keogh River. KEO was a larger stream than the others, and consequently had greater discharge, depth, and width, and faster flowing water (Table 1). KEO also had the largest substrate particles and the least stained water. Mean PC2 scores for fish from all the tributaries were higher than for fish from KEO. Although MO fish had the highest mean PC2 score, the physical habitat at this location was not obviously different from the other tributary sites. With the exception of gradient, all tributary sites were similar in their physical characteristics. WTT was the smallest and steepest site. The two lake outlets, LO and MO, were similar in physical characteristics except LO was more heavily stained, and MO was steeper.

DISCUSSION

We found morphological differences among juvenile coho salmon living in similar tributary habitats. Twelve inter-landmark distances were important in describing shape differences among fish from the various sites. These trusses, mainly related to dorsal, anai, and caudal fin size, and the size of cell 5, the caudal peduncle region, (Fig. 2) in relation to those fins, were significantly correlated with PC2 scores. Both the lengths of the lead rays of the dorsal and anal fins, and the lengths of the bases of these fins, were significantly correlated with PC2 scores, strongly suggesting that the relative sizes of these fins differed among fish from the various locations.

Dorsal and anal fins may be significant for aggressive display purposes; large fins create a large lateral silhouette, resulting in an apparent increase in size during aggressive interactions (Swain and Holtby 1989). Swain and Holtby (1989) noted that the length of the lead rays of the display fins (characters 7-16 and 6-17) were significantly correlated with PC2, however in their study, the base lengths of these fins (6-8, and 7-9) weren't correlated with PC2. Increasing the lengths of the bases of these fins (6-8, 7-9) would further increase the area of the fins during display.

At riverine sites, it appears that variations in fin and caudal peduncle sizes are of greater significance than differences in body depth. In contrast, Swain and Holtby (1989) found little significant variation in cell five when comparing lake and creek origin coho parr, but significant loading of truss 5-6, a measure of body depth. Lake fish were longer and less deep-bodied than creek-origin fish. Body depth measures (3-4, 5-6, 7-8, and 9-10) were of little significance in our study.

Mean PC2 scores differed significantly among fish from our five

locations, which infered that significant morphological differences existed among fish from those five sites. Mean PC2 scores were highest for MO, suggesting larger dorsal and anal fins in fish from that tributary. LO, WT, and WTT had intermediate PC2 scores, and fish from KEO had the lowest scores, indicating smaller fins and a concurrent relative increase in the size of cell 5. There were few obvious relationships between the stream habitat characteristics (Table 1), and mean PC2 scores. MO has a gradual gradient and slow moving water, so one could hypothesize that large fins would be less of a hindrance there than in other, steeper, fast-flowing sites. However, gradient was also shallow and water velocity slow in LO yet PC2 scores for LO were significantly lower than those of fish from MO. KEO had the lowest mean PC2 score. KEO is a flashy riverine environment; discharge fluctuations between 0.15 and 254 m^3sec^{-1} have been recorded (Ward and Slaney 1988). Juvenile coho salmon in KEO may be subjected to much greater flow extremes than fish at the other sites, especially if they remained in the mainstem during fall and winter freshets, however Swales et al. (1988) noted that juvenile Keogh River coho tend to overwinter in the tributaries and lakes, not the mainstem. It is possible that large fins would be a handicap in such an environment, hence selected against.

The observed phenotypic differences among samples may result from phenotypic plasticity, ontogenetic differences, genotypic polymorphisms, actual genetic differences possibly resulting from adaptive variation, or chance alone. Swain and Holtby (1989) noted that if the morphometric and behavioral differences that they observed were due to phenotypic plasticity, the differences must have been induced at an early stage of the life of the fish, since wild fry reared in the laboratory maintained their original morphs for at least two months after capture. Conversely, Winans and Nishioka (1987) observed shape changes over time, particularly in cell 5, within a single population of juvenile coho undergoing smoltification. All the fish examined in our study were of the same age, and unlikely to smolt for six or seven months, however, we are unable to rule out any of the above. To address these concerns adequately, samples should be examined from the same locations, for several consecutive years, to determine whether the observed differences were stable inter-annually, both within and between brood-year lines. Unfortunately, genotypic differences are difficult to demonstrate in coho salmon; coho are apparently less polymorphic at electrophoretically detectable loci than other species of Pacific salmon (Utter et al. 1980).

The occurrence of significant morphological differences among groups of coho parr rearing in different locations raises the possibility that several coho populations may exist within the Keogh River watershed. MO and WT are important spawning streams for Keogh River coho, and coho also spawn in the mainstem Keogh River. We have not observed redds or spawning in WTT, although no barriers to migration exist below our sample site, and small areas of gravel suitable for spawning are available. No redds or adult coho have been observed in LO and we suspect that fish rearing in LO originate from spawning in the Keogh River.

The possible existence of several races of coho salmon within a watershed has implications with respect to management and enhancement activities (Swain and Holtby 1989). Present management strategies typically

treat the coho returning to British Columbia rivers such as the Keogh as a single stock (R. K. Kadowaki, Department of Fisheries and Oceans, Pacific Biological Stn., Nanaimo, B. C., V9R 5K6, pers. comm.). To maintain the genetic diversity and productivity of coho in systems like the Keogh might necessitate a shift to managing the fish returning to the river to spawn as separate populations.

It may not be practical to manage the fishery to protect small populations of coho, but people attempting to enhance small populations should be aware that genetic differences may exist among tributary populations, and practice appropriate broodstock selection. Ferguson (1990) discussed genetic impacts of fish introductions and transfers, including the release of non-local conspecifics, and noted that such liberations may disrupt genetically-based adaptations to particular environments.

We documented distinguishing morphological characteristics among groups of juvenile coho living in different lotic environments within a single watershed. Other workers who found morphological differences among groups of coho studied fish in significantly dissimilar areas (Taylor and McPhail 1985; Swain and Holtby 1989), and the morphological differences they found appeared likely to be specific adaptations to the environment the fish were found in. In our study, the tributary sites were similar to each other, and we were unable to confirm that the morphological differences that we found among tributary fish were adaptations for the environments that the fish were in. Further work is needed to determine why differences are found among groups of fish such as those in our study.

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REFERENCES

Beacham, T. D., and C. B. Murray. 1985. Variation in length and body depth of pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 312-319.

Beacham, T. D., C. B. Murray, and R. E. Withler. 1989. Age, morphology, and biochemical genetic variation of Yukon River chinook salmon. Trans. Am. Fish. Soc. 118: 46-63.

Bisson, P.A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. 117: 262-273.

Bovee, K. D., and T. Cochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: Fisheries. Instream Flow Information Paper No. 3. Fish and Wildlife Service, Office of Biological Services. USFWS/OBS-77/63. 49pp

Ferguson, M. M. 1990. The genetic impact of introduced fishes on native species. Can. J. Zool. 68: 1053-1057.

Fleming, I. A. and M. R. Gross. 1989. Evolution of adult female life history and morphology in a Pacific salmon (Coho: Oncorhynchus kisutch). Evolution 43: 141-157.

Fournier, D. A., T. D. Beacham, B. E. Riddell, and C. A. Busack. 1984. Estimating stock composition in mixed stock fisheries using morphometric, meristic, and electrophoretic characteristics. Can. J. Fish. Aquat. Sci. 41: 400-408.

Hart, J. L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. No. 180.

Hjort, R. C., and C. B. Schreck. 1982. Phenotypic differences among stocks of hatchery and wild coho salmon, Oncorhynchus kisutch, in Oregon, Washington, and California. Fish. Bull. 80: 105-119.

Humphries, J. M., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291-308.

Irvine, J. R., and B. R. Ward. 1989. Patterns of timing and size of wild coho salmon (Oncorhynchus kisutch) smolts emigrating from the Keogh River watershed on northern Vancouver Island. Can. J. Fish. Aquat. Sci. 46: 1086-1094.

Ricker, W. E. 1970. Hereditary and environmental factors affecting certain salmonid populations, p19-160. In: Simon, R. C. and Larkin, P. A. [ed.]. H. R. MacMillan lectures in fisheries: The stock concept in Pacific Salmon. University of British Columbia Press, Vancouver, B. C.

Riddell, B. E., and W. C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. 38: 308-320.

SAS Institute Inc. 1988a. SAS procedures guide: Release 6.03 edition. Cary, NC: SAS Institute Inc., 1988. 441pp.

SAS Institute Inc. 1988b. SAS/STAT user's guide, 6.03 edition. Cary, NC: SAS Institute Inc., 1988. 1028pp.

Strauss, R. E., and F. L. Bookstein. 1982. The truss: body form reconstruction in morphometrics. Syst. Zool. 31: 113-135.

Swain, D. P., and L. B. Holtby. 1989. Differences in morphology and behaviour between juvenile coho salmon (Oncorhynchus kisutch) rearing in a lake and its tributary stream. Can. J. Fish. Aquat. Sci. 46: 1406-1414.

Swales, S. 1987. The use of small wire-mesh traps in sampling juvenile salmonids. Aquaculture and Fish. Manage. 18: 187-195.

Swales, S., F. Caron, J. R. Irvine, and C. D. Levings. 1988. Overwintering habitats of coho salmon (Oncorhynchus kisutch) and other juvenile salmonids in the Keogh River system, British Columbia. Can. J. Zool. 66: 254-261.

Taylor, E. B., and J. D. McPhail. 1985. Variation in body morphology among British Columbia populations of coho salmon, Oncorhynchus kisutch. Can. J. Fish. Aquat. Sci. 42: 2020-2028.

Utter, F. M., D. Pail, S. Grant, G. Milner, J. Seeb, and L. Wishard. 1980. Population structure of indigenous salmon species of the Pacific Northwest, p. 285-304. In McNeil, W. and Himsworth, D. [ed.] Salmonid ecosystems of the North Pacific. University of Oregon Press, Corvallis, OR

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt to adult survival of Keogh River steelhead trout (Salmo gairdneri) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45: 1110-1122.

Winans, G. A. 1984. Multivariate morphometric variability in Pacific salmon: technical demonstration. Can J. Fish. Aquat. Sci. 41: 1150-1159.

Winans, G. A., and R. S. Nishioka. 1987. A multivariate description of change in body shape of coho salmon (Oncorhynchus kisutch) during smoltification. Aquaculture 66: 235-245.

Table 1. Physical characteristics of the study sites; Long Outlet Stream (LO), Misty Outlet Stream (MO), West Tributary (WT), West Tributary Tributary (WTT), and the mainstem Keogh River (KEO).

	LO	MO	WT	WTT	KEO
Depth range (cm)	1-70	1-30	1-30	1-20	1-100
Width range (m)	.5-5	1-5	3-8	.5-3	3-18
Velocity ($m.sec^{-1}$)	<.2	<.2	<.2	0-.4	0-.7
Discharge (m^3sec^{-1})	~.03	~.03	~.03	~.01	~.13
Substrate particle type	Sand; coarse gravel	Coarse gravel; large cobble	Coarse gravel; large cobble	Sand; large cobble; small boulder	Coarse gravel; medium boulder
Temperature (°C)	20	17	18	20	18
Staining[1]	0.103	0.083	0.088	0.067	0.042
Gradient (percent)	<0.5	1.0	1.1	3.2	0.6

[1] Absorbance at 400 nm.

Table 2. Mean principal component loadings by truss, for juvenile coho salmon from four Keogh River tributaries and the Keogh River mainstem.

Cell	Character	PC1 Score	PC2 Score	
1	1-2	0.165	0.030	
	1-3	0.149	0.022	
	2-3	0.186	0.032	
	1-4	0.182	-0.122	
	2-4	0.162	-0.225	*
2	3-4	0.187	0.037	
	3-5	0.183	0.052	
	4-5	0.183	0.123	
	3-6	0.188	-0.044	
	4-6	0.178	0.100	
3	5-6	0.188	0.012	
	5-7	0.167	-0.046	
	6-7	0.189	0.020	
	5-8	0.185	0.001	
	6-8	0.170	0.156	*
4	7-8	0.187	-0.021	
	7-9	0.164	0.206	*
	8-9	0.186	0.026	
	7-10	0.186	-0.001	
	8-10	0.179	-0.078	
5	9-10	0.185	0.014	
	9-11	0.131	-0.490	*
	10-11	0.176	-0.182	*
	9-12	0.169	-0.318	*
	10-12	0.171	-0.213	*
6	11-12	0.171	-0.199	*
	11-13	0.177	0.148	*
	12-13	0.187	0.057	
	11-14	0.188	0.043	
	12-14	0.178	0.177	*
	13-14	0.175	0.014	
other	6-17	0.132	0.320	*
	7-16	0.104	0.451	*

* variables with significant (P<.05) correlations with PC2

Table 3. Mean PC2 scores, SE, and groupings as determined by Tukey's test for the sample locations.

Sample Site	PC2 Score	SE	Tukey Grouping
MO	1.097	0.154	a
WT	0.105	0.159	b
LO	-0.138	0.148	b
WTT	-0.160	0.204	b
KEO	-1.099	0.150	c

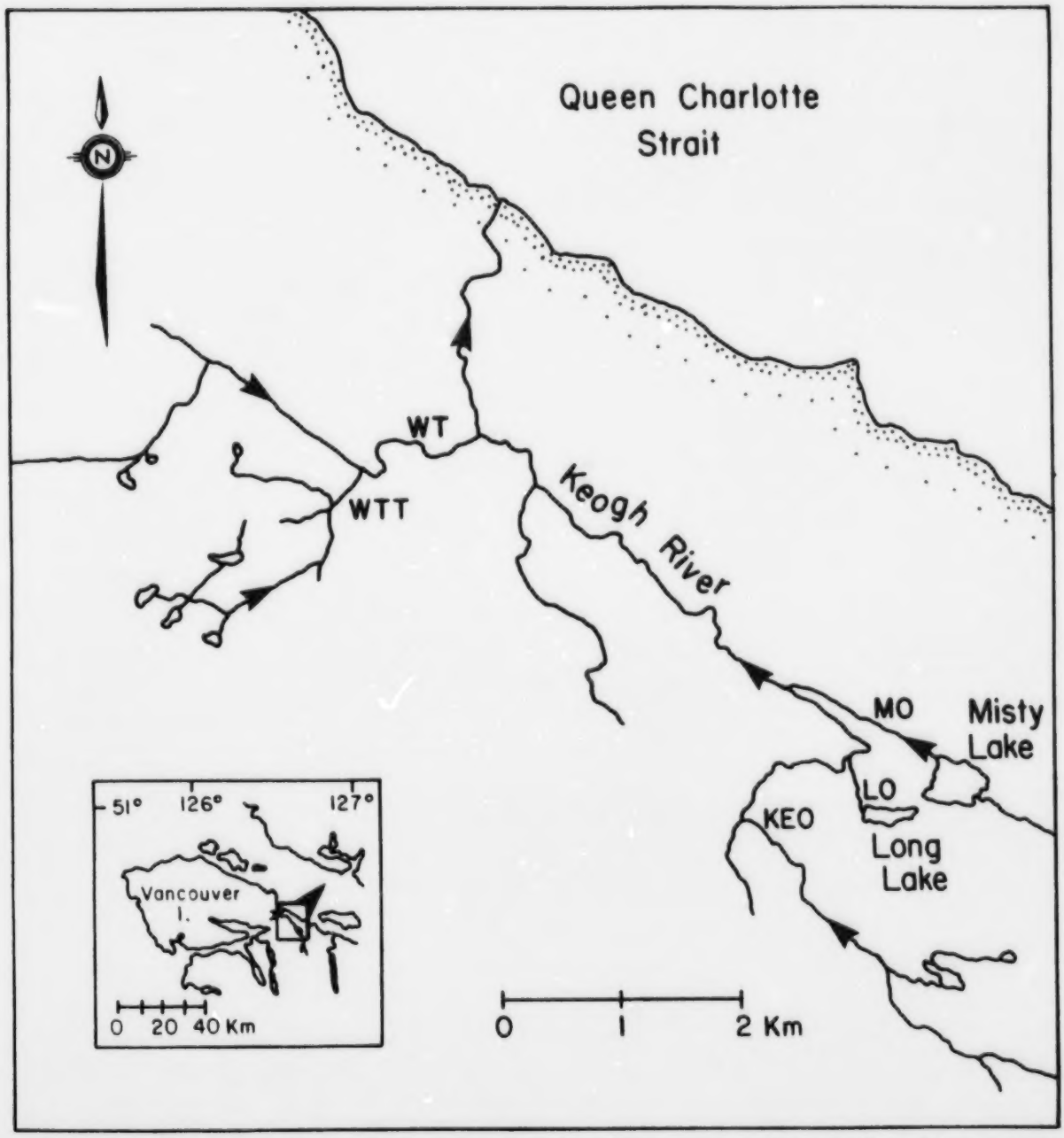

Fig. 1. The Keogh River drainage. Sample sites were: Long Outlet Stream (LO), Misty Outlet Stream (MO), West Tributary (WT), West Tributary Tributary (WTT), and the mainstem Keogh River (KEO).

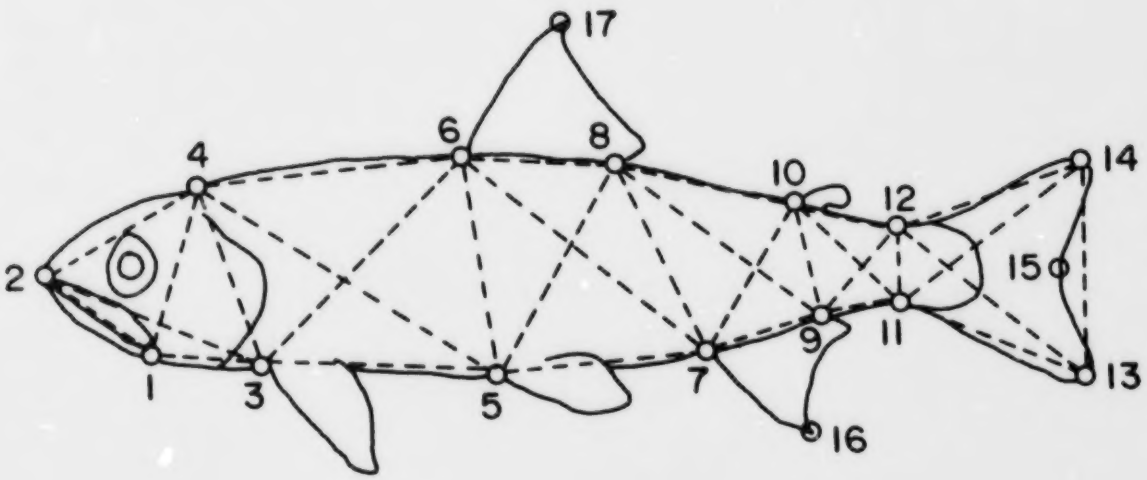

Fig. 2. Locations of the landmarks used to calculate the truss network (broken lines), lengths of the lead rays of the dorsal and anal fins, and forklength. Modified from Winans (1984).